THE TAXONOMIC RELATIONSHIP BETWEEN PICEA GLAUCA (MOENCH) VOSS AND P. ENGELMANNII PARRY[1]

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For many years botanists and foresters have been puzzled and frustrated by the spruce complex in British Columbia, particularly the plexus centering around *Picea glauca* (Moench) Voss (White spruce) and *P. engelmannii* Parry (Engelmann's spruce). In the northern parts of the province *P. glauca* appears in its typical form and is a clear-cut entity. At higher altitudes in the southern interior of the province *P. engelmannii* may be found in equally characteristic form. Unfortunately, between these two easily distinguishable extremes there is a great range of intermediates. The taxonomic, and hence the nomenclatural, disposition of these intermediates is the substance of the present paper.

Materials studied were collected largely at Banff, in the Upper Columbia Valley, and in the Cranbrook-Moyie Lake area. This southeastern region of the province and adjacent Alberta was selected because here the problem raised by the intermediate forms of spruce is particularly acute. Collections were made with the primary purpose of gaining a statistical picture of the variability between individual trees of certain mensural characters of leaves and cones. It was felt that only when the extent of variation within the individual was established, could one proceed with confidence to generalizing from small samples drawn from many trees.

Materials were collected from about seventy randomly selected trees. In case the degree of shading might produce constant differences, cones and twigs with needles were taken from both the north and south side of trees. Needles were also collected from both vegetative and reproductive shoots. Statistical analysis showed no significant difference between samples from the north and south side, nor between needles from reproductive and vegetative twigs. In the present report therefore this distinction is not maintained.

The difficulty of making accurate measurements of curved leaves was overcome by boiling them for five minutes to render them pliable so that they could be straightened out. Spreading of the scales in dry cones also offered complications for measurement but these complications were also overcome by boiling the cones until they sank. By this time the scales had contracted and were closely appressed in the cone. It was established that prolonged boiling produced no further change in dimensions.

Mention may be made of the findings on intra-tree variability. Needle lengths, with means of the order of 13.5 mm. and standard deviations of about 2 mm. showed coefficients of variability ranging from about 11 to 20. Cone diameters with means of the order of 13.5 mm. have standard deviations of slightly over 1 mm. with a range in the coefficients of vari-

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ability from 6 to 10. Cone lengths were about 42 mm., with standard deviations about 3.5 mm. and variability with coefficients about the same as for diameters.

One can conclude then that needle lengths are very variable on the same tree and that a large number would have to be measured in order to obtain a statistically satisfactory mean value. Cones, on the other hand, are much more uniform in dimensions and so smaller samples per tree would be acceptable.

The most obvious difference between Engelmann's and White spruce is in the cone scale. Those of the former are thin and somewhat papery, wedge-shaped with wavy to erose margins, and commonly erose to truncate at the apex. The scales of the White spruce on the other hand, are obovate-triangular, somewhat stiff with entire margins, the apex being rounded or somewhat flattened, not erose. It was possible to interpolate three classes of intermediates between these extremes. In the accompanying tables the five cone type classes are numbered in Roman numerals with *P. engemannii* I and *P. glauca* V. Table 1 shows the means and standard deviations of cone diameters and lengths for the five cone type classes. The differences between the means of diameter are not reliable while the differences in mean length of types I and V is reliable at the level of .01. The erratic means of length for types in II, III and IV are presumably due to inadequacy of the samples. This, however, is a matter that requires further investigation.

TABLE 1. Relationship between cone dimensions and cone type in *Picea engelmannii, P. glauca,* and intermediates.*

Cone type	Diameter				Length			
	M	SD	N	n	M	SD	N	n
I	13.7	1.13	14	521	45.0	3.11	14	518
II	14.0	1.12	12	349	46.1	6.57	11	328
III	13.4	1.03	6	207	41.8	3.72	6	199
IV	13.6	1.28	6	368	43.1	3.00	6	377
V	13.4	1.27	21	1449	41.4	3.96	21	1491

* I represents *P. engelmannii,* V, "*P. glauca,*" II-IV, intermediates. M = mean (in mm.), SD = standard deviation (in mm.), N = number of trees sampled, n = number of cones measured.

Analysis of needle length showed no significant differences between the means for the different cone types. Engelmann spruce needles, however, tended to be straight and slender, acuminate and somewhat square in cross-section, while those of White spruce were firmer, often curved and rounded at the apex, tending to be dorsiventrally flattened or triangular in section. Needles with these characteristics in other combinations were classed as "intermediates." Table 2 shows the relationship found between leaf type and cone type. It is apparent that foliage characters are not correlated with cone types and are probably due to the independent segregation of several genes.

TABLE 2. Relationship between leaf type and cone type in *Picea engelmannii, P. glauca,* and intermediates.*

Leaf types	Cone types I	II	III	IV	V	N
'engelmannii'	9	7	5	....	....	21
intermediate	12	4	4	7	8	35
'glauca'	....	....	....	1	13	14
Totals	21	11	9	8	21	70

* I represents *P. engelmannii,* V, *P. glauca,* II-IV, intermediates. N = number of trees sampled.

The relationship between the indumentum of the twigs and cone types was also studied. Twigs of White spruce are characteristically glabrous, while those of Engelmann's spruce have a short, crisp pubescence. In Table 3 it can be seen that all cone types may be borne on trees with pubescent twigs, except that cone type V has an equal chance of being borne on a tree with glabrous twigs. One can speculate that the development of indumentum is controlled by a single pair of genes and that "pubescence" is dominant.

TABLE 3. Relationship between indumentum of twigs and cone in *Picea engelmannii, P. glauca,* and intermediates.*

Twigs	Cone types I	II	III	IV	V	N
Pubescent	21	10	9	8	11	59
Glabrous	....	1	....	....	10	11
Totals	21	11	9	8	21	70

* I represents *P. engelmannii*-type, V, *P. glauca*-type, II-IV, intermediates. N = number of trees sampled.

It is apparent that White and Engelmann's spruce are very much alike and that even such diagnostic features as mean cone length, and shape and character of the scales are merely the extremes of a series of intermediates. Both 'engelmanii' and 'glauca' needle types are found on trees with 'intermediate' type cones and 'intermediate' type needles may be associated with any type of cone. Glabrous twigs have only been found on trees with 'glauca' cones but, on the other hand, there is an equal chance that the twigs on such trees will be pubescent. On several occasions in the past it has been commercially important to try to distinguish lumber cut from these two spruces. No differentiating histological details have been found and Barton and Gardner (1957), using partition chromatography in addition to infra-red and ultra-violet spectrographic methods, failed to establish any chemical differences between the woods.

Wright (1955) has examined in considerable detail the question of interspecific hybrids in *Picea*. In his paper he attempts "to correlate species crossability with geographic distribution, morphology, and phylogeny." He examined thirty-one species with respect to fifty-one characters that show differences between some or other of these species. The majority of the characters, of course, do not lend themselves to measurement and are to quite an extent subjective. It is regrettable that Wright's observations were not analyzed statistically. Had they been, the relationship between *P. glauca* and *P. engelmannii* would likely have appeared very much closer than he concludes.

Wright (l. c.) has made some investigation of hybridizing between White and Engelmann spruce. Using a hybridity index, he shows that very considerable introgression is taking place over a wide area extending from latitude 51° to 58° N. and between longitude 109° to 124° W. That these intermediates are almost certainly of hybrid origin is borne out by his report of successful reciprocal crosses between the two species.

Garman (1957) has made a detailed morphological and distributional study of spruce populations in British Columbia. Using a "morphological index" on which pure *P. glauca* rates 6 and pure *P. engelmannii* rates 18, he shows the very extensive geographic area occupied by intermediates on this scale. This index has apparently proven useful in distinguishing populations, but its value would be greatly enhanced if the mensurable characters had been treated statistically. Only average values and ranges of measurement are given and, as the latter frequently overlap, their significance cannot be evaluated.

In the opinion of the present author, the phylogenetic relationship between *P. glauca* and *P. engelmannii* is best indicated by regarding them as subspecies of a single species and so the following changes in status are proposed. According to the provisions of Article 57 of the International Code of Botanical Nomenclature (Lanjouw 1956) *Picea glauca* (Moench) Voss, which has priority, becomes the legitimate name when the two species are combined into one.

PICEA GLAUCA (Moench) Voss subsp. **glauca**

Abies canadensis Mill. Gard. Dict. Ed. 8, Abies No. 4, 1768; *nomen confusum*
Pinus glauca Moench, Verzeichn. Baeume Weissenst. 73. 1785
Pinus alba Ait. Hort. Kew. 3:371. 1789
Picea laxa Sargent, Gard. and For. 2:496. 1889
Picea glauca (Moench) Voss, Mitt. Deutsch. Dendr. Ges. 1907:93. 1907
Picea glauca var. *porsildii* Raup, Sargentia 6:102. 1947

PICEA GLAUCA (Moench) Voss subsp. **engelmannii** (Parry) stat. nov.

Abies engelmanni Parry, Trans. Acad. St. Louis 2:122. 1863; *nomen nudum*
Picea engelmanni Parry ex Engelmann; Trans. Acad. St. Louis 2:212. 1863
Picea columbiana Lemmon, Gard. and For. 10:183. 1897

There is little doubt that *Picea glauca* var. *albertiana* (S. Brown) Sargent (*Picea albertiana* S. Brown, Torreya 7:126. 1907) is based on an individual of the hybrid swarm between subsp. *glauca* and subsp. *engelmannii* and in consequence this name should no longer be perpetuated. When reference is made to these hybrid intermediates it should be done by employing a formula as provided by Article H.2 of the International Code with particular attention to the "Note."

Goodman (1950), in describing his *P. engelmannii* var. *glabra,* almost certainly had at hand a biotype of Engelmann's spruce that showed the result of the introgression of genes from the glabrous White spruce.

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FIELD STUDIES OF NATURAL HYBRIDIZATION IN THE OREGON SPECIES OF IRIS L. SUBSECTION CALIFORNICAE DIELS

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Smith and Clarkson (1956) have discussed the cytological aspects of hybridization in *Iris,* subsection *Californicae.* They reported that, with the exception of *I. tenuis* Wats., which has been removed to a new subsection (Clarkson, 1958), all the members of the subsection studied had a uniform chromosome morphology, and all contained a diploid number of forty. Fertile hybrids were produced experimentally without difficulty and all were highly fertile except that hybrids involving *I. tenuis* as a parent could not be produced. This paper will discuss some natural hybrids of those taxa occurring in western Oregon and will propose certain nomenclatural revisions. Because the subsection was treated taxonomically by Foster (1937), conventional citations will not be included except for taxa described since that time.

Distinguishing Characteristics. Aside from the usual characteristics of the genus *Iris,* the members of the subsection *Californicae* are distinguished by a usually deltoid stigma; D-shaped, cubical or ovoid seeds; the absence of foliaceous stem leaves; and tough basal leaves which are reddish at base. A number of characteristics have been used for distin-